TWO FOSSIL SPECIES OF *METROSIDEROS* (MYRTACEAE) FROM THE OLIGO-MIOCENE GOLDEN FLEECE LOCALITY IN TASMANIA, AUSTRALIA

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SUMMARY

- *Premise of the study:* The capsular-fruited genus *Metrosideros* (Myrtaceae) is one of the most widely distributed flowering plant genera in the Pacific, but is extinct in Australia today. The centre of geographic origin for the genus, as well as the reason and timing for extinction in Australia, remain uncertain. In this paper, fossil *Metrosideros* fruits from the newly discovered Golden Fleece fossil flora in the Oligo-Miocene of Tasmania, Australia, are identified and described, shedding further light on these problems.
- *Methods:* Standard paleopalynolgoical techniques were used to date the fossil bearing sediments. Scanning Electron Microscopy (SEM) and an auto-montage camera system were used to take high-resolution images of fossil and extant fruits taken from herbarium specimens. Fossils are identified using a nearest living relative approach.
- *Key Results:* The fossil bearing sediments are palynostratigraphically dated as being *Proteacidites tuberculatus* Zone Equivalent (ca. 33–16 Ma) in age, and provide a confident Oligo-Miocene age for the macrofossils. Two new fossil species of *Metrosideros* are described, and are here named ***Metrosideros dawsonii***, sp. nov. and ***Metrosideros wrightii***, sp. nov.
- *Conclusions:* These newly described fossil species of *Metrosideros* provide a second record of the genus in the Cenozoic of Australia, placing them in the late Early Oligocene to late Early Miocene. It is now apparent that not only was *Metrosideros* present in Australia, where the genus is now extinct, but that at least several *Metrosideros* species were present during the Cenozoic. These fossils further strengthen the case of an Australian origin for the genus.

Key words: Cenozoic; fossil; Golden Fleece; Metrosideros; Myrtaceae; Oligocene; Miocene; Oligo-Miocene; Tasmania; fossil record; capsular fruit;

INTRODUCTION

Recently described fossils of *Metrosideros,* with affinities to subgenus *Metrosideros* from the Late-Eocene to Early-Oligocene of Australia have helped to understand one of the great biogeographic puzzles of the capsular-fruited Metrosidereae which is the absence of this tribe from Australia despite a widespread distribution around the Pacific (Fig. 1), and a clear adaptation for long distance dispersal in at least subgenus *Metrosideros* (Tarran et al. 2016). These fossils help to interpret the current absence of the *Metrosidereae* from Australia as being a result of extinction, rather than an absence of dispersal from some other landmass, such as New Zealand.

While these fossils contribute to our understanding of the paleobiogeography of the group, other pertinent questions still remain surrounding; **1)** the geographic origin of the genus, **2)** the deep infrageneric relationships within *Metrosideros,* and **3)** the poorly resolved relationships with the other closely related tribes Backhousieae, Kanieae, Myrteae, Syzygieae and Tristanieae (Pillon et al. 2015). Further fossil records of this group may help to reveal key insights into these problems.

The delimitation of genera in the tribe Metrosideaeae (sensu Wilson et al. 2005) has been the subject of much debate, with the number of genera recognized varying from four (eg, Wilson et al. 2005) to only one (Pillon et al. 2015). *Metrosideros* itself has often been divided into two subgenera, *Metrosideros* and *Mearnsia*, on the basis of vegetative and inflorescence characters (eg, Dawson 1992). However, published analyses have shown that while the subgenus *Metrosideros* is monophyletic, the subgenus *Mearnsia* is polyphyletic (Wright et al. 2000, Papadopulos et al. 2011, Pillon et al. 2015). In terms of understanding the paleobiogeography of the genus, the two morphology-based subgeneric groupings may still hold some value, since it is the subgenus *Metrosideros* that has dispersed so widely around the Pacific. Although the formerly recognized subgenus *Mearnsia* (which encompassed most of the remaining species in the genus) may no longer be taxonomically valid, the species within it are less widely distributed around the Pacific (Wilson 1996), occurring only on the Gondwanic landmasses of New Zealand, New Caledonia, New Guinea, as well as the Solomon Islands and the Philippines (Fig. 1A, with one outlier in South Africa, to be discussed later). As such it might be considered that they are not as well adapted for long distance dispersal as are some species in subgenus *Metrosideros.* Discovery of fossils of subgenus *Mearnsia* in Australia, in conjunction with the previously described subgenus *Metrosideros* fossils by Tarran et al. (2016) might be considered further evidence for an Australian origin for the genus.

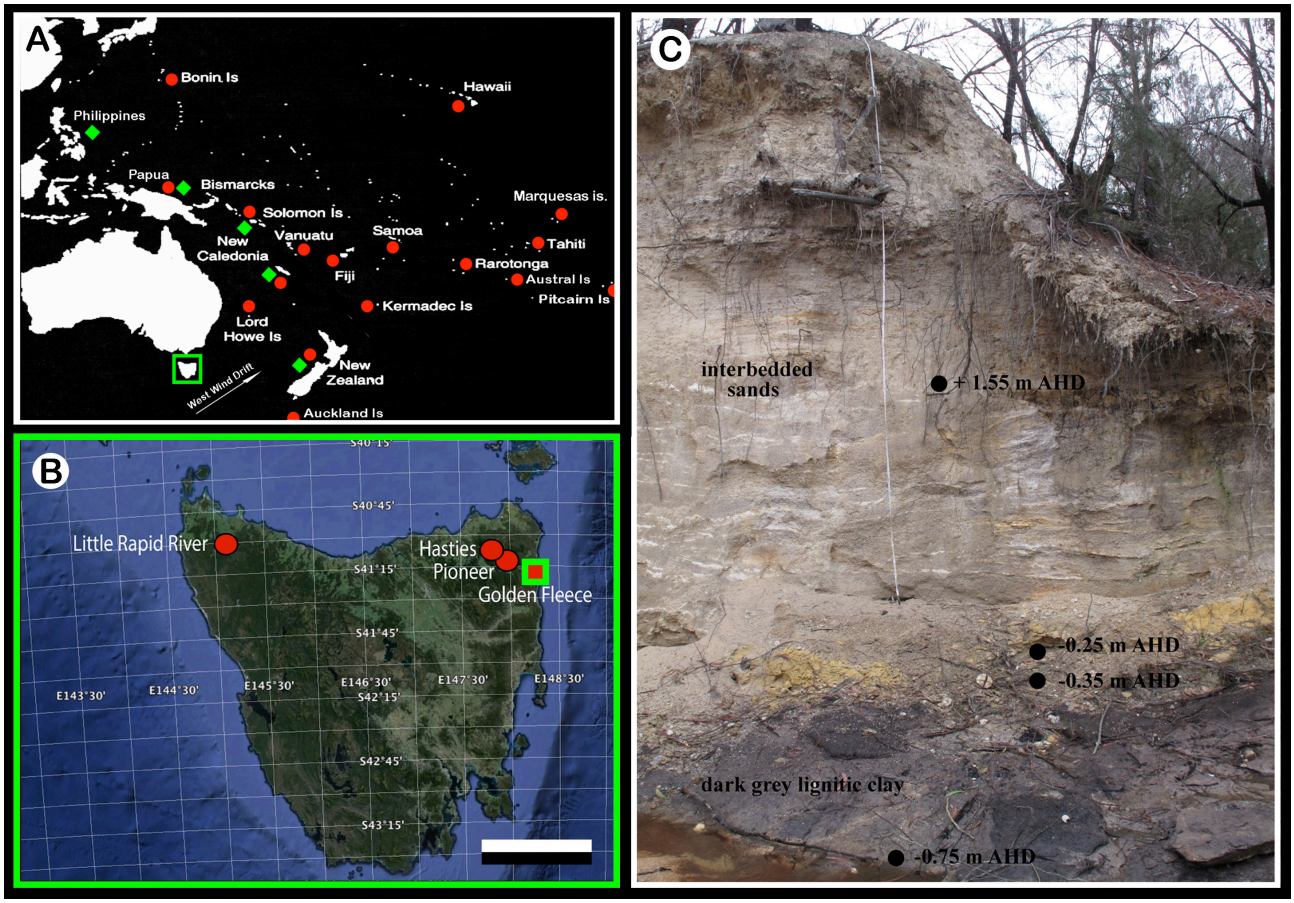

FIGURE 1 – (A) Distribution of *Metrosideros* subg. *Metrosideros* (red circles) and subg. *Mearnsia* (green diamonds) in the Pacific, based on maps from Wright et al. (2000, 2003) with a question mark in Australia indicating their absence from the Australian mainland. Note that this map doesn't include the distribution of the South African *Metrosideros angustifolia* of subg. *Mearnsia,* or the South American *Tepualia stipularis,* which has been placed in *Metrosideros* by the most recent circumscription of the genus by Pillon (et al. 2015) extending the range of distribution of the genus. **(B)** Map of fossil sites in Tasmania. The Golden Fleece rivulet is located in the far northeast. The Early Oligocene Little Rapid River (LRR) site, where the fruits and flowers of *M. leunigii* were discovered, is in the northwest; leaves were found at the Middle-Late Eocene Hasties site in the northeast; and a single leaf was found at the late Oligocene/Early Miocene Pioneer site. Scale bar = approx.100 km. Map data: Google, DigitalGlobe 7.1.2.2041. **(C)** Photograph of the fossil bearing outcrop at the Golden Fleece Rivulet, showing the interbedded sands of Pliocene/Pleistocene age overlying the dark grey lignitic clays. The four points at +1.55 m, -0.25 m, -0.35 m, and -0.75 m indicate the horizons from which sediment samples were taken for palynostratigraphic analysis and age control. The fossils occur within the dark grey lignitic clays between the -0.35 m and -0.75 m sample points.

A new record of *Metrosideros* fruits is reported here from carpological remains in late-Early-Oligocene to late-Early-Miocene (henceforth Oligo-Miocene) age sediments from the fossil bearing Golden Fleece Rivulet strata in northeastern Tasmania (Fig. 1 B,C). These are the first macrofossils published from the Golden Fleece rivulet.

Metrosideros-type pollen has not been recorded from the fossil bearing sediments, however fossil Myrtaceae pollen (nearest living relatives in brackets) are present in low abundance: *Myrtaceidities eucalyptoides* (*Eucalyptus* sensu lato), *M. parvus-mesonesus* (Myrtaceae), and *M. verrucosus* (*Rhodamnia*-type). The most recent palynological survey of the extant Myrtaceae by Thornhill et al. (2012) suggests that, compared with other tribes of Myrtaceae, *Metrosideros* pollen are not dissimilar to pollen of Melaleuceae, Syzygieae, Eucalypteae and Xanthostemoneae, and so at least two of these pollen types could plausibly also represent *Metrosideros*. The equivocal affinity of fossil Myrtaceae pollen highlights the importance of macrofossil evidence in interpreting the paleobiogeography of this family.

In this paper two new fossil species of *Metrosideros* are described from the Oligo-Miocene of Tasmania, Australia, and compared with fruits of *Metrosidereae* from around the Pacific, as well as with other strikingly similar Miocene fossil fruits from New Zealand that were reported by Pole (2008), but which were not formally described as new fossil species.

MATERIALS & METHODS

Fossil Sites and Setting —

The *Metrosideros* fossil fruits are preserved in a thin, lignitic clay which outcrops at water level on the northern bank of the Golden Fleece Rivulet [41^0 18' 06"S 148^0 10' 03" 50 m elevation] ca. 5 km west of St Helens on the northeast coast of Tasmania. The stream is located within a former course (Thureau's Deep Lead) of the Georges River (Georges River Palaeovalley) incised into Silurian-Early Devonian marine sediments (upper Mathinna Supergroup) and Devonian granitic rocks. The fossiliferous outcrop is partly buried under sands and silts from talus dumped into the rivulet during tin mining operations in the nineteenth century.

Lithostratigraphy: Sediments exposed in the ca. 4.75 m high cliff forming the stream bank comprise an upper section of friable fine to coarse ripple-bedded sands and cross-bedded yellow silts unconformably overlying grey silty clays, which become darker in colour and clay-rich down section (Figure 1C). A thin interval of laminated lignites appears to separate the two units at one point in the outcrop.

Topography and vegetation: Topographic relief in the St Helens district is subdued, with elevations exceeding 100-250 m above sea level only in the headwaters of the rivulet and in hills to the south of the township.

Much of the present-day forest vegetation is post-mining regrowth but remnant stands are of low-medium open forest types, especially *Eucalyptus sieberi* dry sclerophyll forest and woodland, occurring on more fertile sites.

Age control —

Samples from the sediments taken at four intervals up the cliff (-0.70 m, -0.35 m, -0.25 m and +1.55 m on the Australian Height Datum, AHD) were dated using time distribution data from the Gippsland and Murray Basins in southeast Australia, and northwest Tasmania (Macphail & Hill 1994, Macphail 1999, Partridge 1999, (Fig. 1C; Table 1). The data confirm two (possibly three) sedimentary units are present in the cliff section although all have been contaminated with modern exotic pollen, e.g. *Pinus*.

Table 1: Pollen and spore sample data from the exposed cliff face at the Golden Fleece Rivulet.

SAMPLE	DEPTH	SAMPLE	LITHOLOGY	YIELD	
				Organic yield	Spore-pollen
GFC2	+1.55 m	outcrop	charcoal-rich silt	high	medium
GFC4	–0.25 m	outcrop	light grey silt	low	very low
DATUM (top of organic silty clay)					
GFC3	–0.35	outcrop	dark grey organic silty clay	very high	abundant
GFC1	–0.75	outcrop	dark grey organic clay	very high	abundant
Water level at time of sampling (–0.75 m)					

The *Metrosideros* macrofossils were recovered from the dark grey lignitic clays between –0.35 to –0.75 m AHD (Fig. 1C), are dated as Early Oligocene to Early Miocene *Proteacidites tuberculatus* Zone Equivalent (ca. 33–16 Ma) using the combined microfossil evidence from both samples. Key age-diagnostic taxa are *Cyatheacidites annulatus* (*Lophosoria*) (Fig. 2D) and *Mutisiapollis* cf. *patersonii* (*Mutisia*), which first occurs in the Early Oligocene Lower *Proteacidites tuberculatus* Zone in the Gippsland Basin and northwest Tasmania respectively, and *Dryptopollenites retequetrus* (extinct angiosperm) and *Proteacidites rectomarginis* (extinct Proteaceae) (Fig. 2F) which last occurs in the Upper *Proteacidites tuberculatus* Zone in the Gippsland Basin and northwest Tasmania, respectively. This age range can be narrowed to ca. 31.5–19 Ma if the absence of other age-diagnostic taxa such as *Granodiporites nebulous* (which last occurs in the Lower *P. tuberculatus* Zone) and *Acaciapollenites myriosporites* (which first occurs in the Upper *P. tuberculatus* Zone) is regarded as reliable evidence.

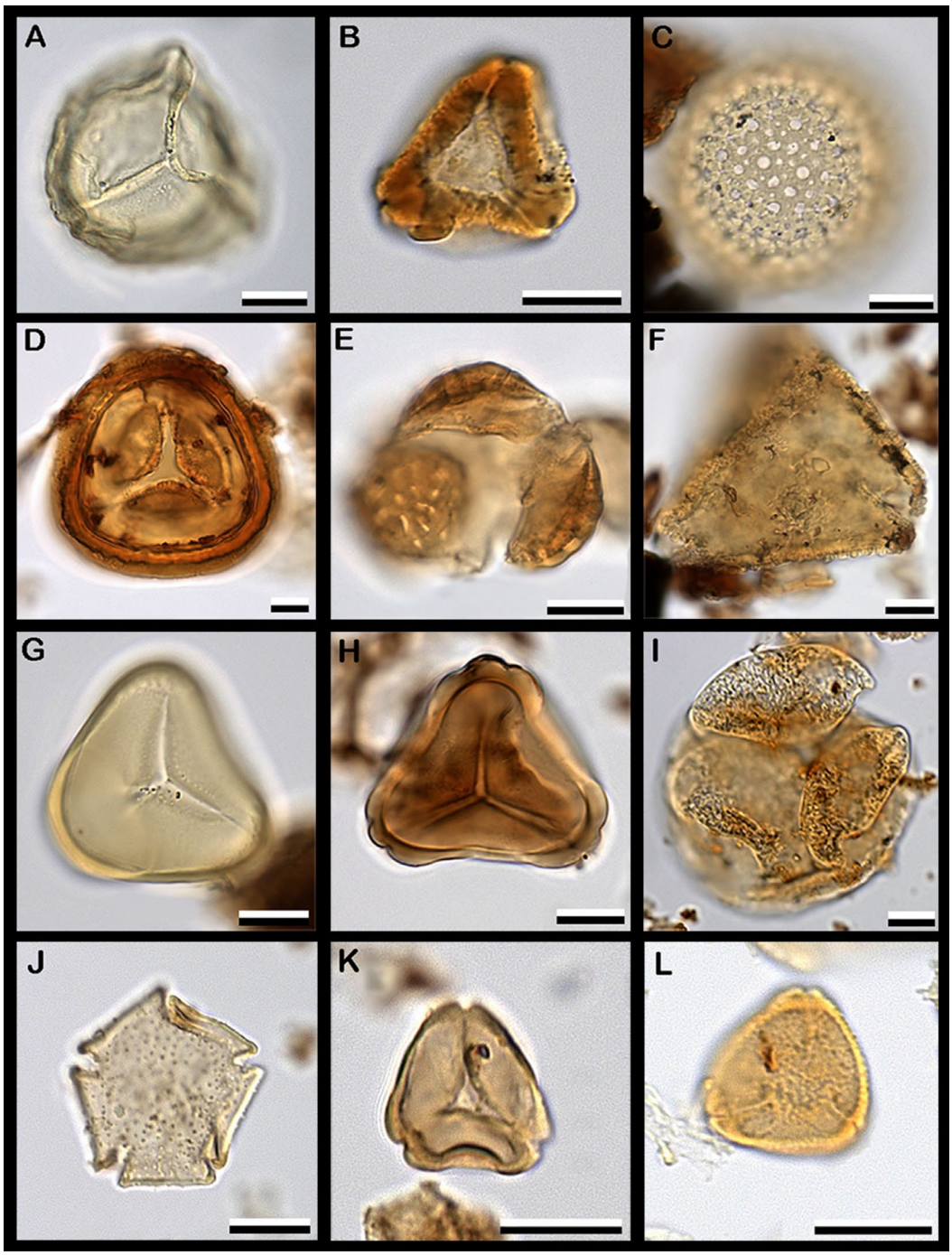

FIGURE 2 – Selected taxa used for biostratigraphic age constraint of the fossil bearing sediments, with NLR in parentheses - **(A)** *Densoisporites implexus* (*Selaginella uliginosa*). Spore in high (proximal) optical view. +1.55 m AHD. **(B)** *Myrtaceidites* cf. *lipsis* (*Eucalyptus spathulata*-type). Pollen in median optical view. +1.55 m AHD. **(C)** *Thymelaepollis* sp. (*Pimelea* sp.). Pollen in high optical view. +1.55 m AHD. **(D)** *Cyatheacidites annulatus* (*Lophosoria*). Spore in median optical view showing diagnostic three contact pads on proximal surface. – 0.75 m AHD. **(E)** *Dryadopollis retequetrus* (extinct angiosperm). Pollen in oblique lower optical view showing coarsely reticulum in mesocolpial areas. – 0.35 m AHD. **(F)** *Proteacidites rectomarginis* (extinct Proteaceae). Corroded pollen in median optical view showing parallel groves in exine around the apertures. – 0.75 m AHD. **(G)** *Cyathidites australis* (*Cyathea*). Spore in high optical view. – 0.25 m AHD. **(H)** *Matonisporites ornamentalis* (*Dicksonia*). Spore in median optical view. – 0.75 m AHD. **(I)** *Dacrycarpites australiensis* (*Dacrycarpus*). Pollen (proximal surface uppermost) showing three large sacci. – 0.35 m AHD. **(J)** *Nothofagidites emarcidus-heterus* (*Nothofagus* subgenus *Brassospora*). Pollen in median optical view. – 0.35 m AHD. **(K)** *Myrtaceidites parvus-mesonesus* (Myrtaceae). Pollen in median optical view. – 0.35 m AHD. **(L)** *Myrtaceidites verrucosus* (*Rhodamnia*-type). Pollen in high optical view showing diagnostic verrucate ornamentation. – 0.75 m AHD.

Immediately overlying the fossil bearing sediments is a light grey sandy silt at –0.25 m AHD which does not preserve macrofossils. It is unclear whether the sample comes from a thin but discrete silt overlying the lignitic clays unit or the basal unit in the overlying sands. Assuming the 19 specimens of *Nothofagidites emarcidus-heterus* (*Nothofagus* subgenus *Brassospora,* Fig. 2J) are *in situ*, the very sparse microflora is no more recent than the Late Pliocene but the maximum age cannot be determined due to the very low yield.

The topmost unit in the cliff section are sands and silts which preserve fossil pollen and spores, but not macrofossils. A sample at +1.55 m AHD yielded a mixed-age microflora with fossil species that first occur in southeastern Australian in the Early Pliocene (5.3 Ma) and beomes extinct in the Early Pleistocene (1.8 Ma), e.g. *Myrtaceidites* cf. *lipsis* (*Eucalyptus spathulata*-type, Fig. 2B), and species which first occur in the Early Pleistocene (<2.59 Ma), e.g. *Leucopogon*-type (*Leucopogon*) and *Thymelaepollis* sp. (*Pimelea,* Fig. 2C) This unit is likely to represent aggradation in the Golden Fleece Rivulet of talus derived from tin-mining in the area..

The combined evidence provides a confident Oligo-Miocene age for *Metrosideros* macrofossils preserved in the dark grey lignitic clays between -0.35 m and – 0.75 m AHD, which is clearly delineated from the overlying sediments, and securely dates any further macrofossils to be described from this site.

Depositional environment and paleovegetation —

The microflora recovered from the macrofossil-bearing organic clays is dominated by fungal spores, (165-310%, with percentages calculated relative to the pollen sum, see materials and methods) and tree pollen taxa, notably *Nothofagidites emarcidus-heterus* (Fig. 2J, 59-65%) and *Podocarpidites* (*Podocarpus-Prumnopitys*), whilst wetland herbs such as *Cyperaceaepollis* (Cyperaceae) and freshwater algal cysts are virtually absent. The relative abundance of these taxa compared to the low relative abundance of spores of shade-intolerant tree-ferns such as *Matonisporites ornamentalis* (Fig 2H) and *Cyathidites* spp. (Cyatheaceae, eg. Fig. 2D) is best interpreted as evidence that the organic clay accumulated in a depression within the closed canopy of Podocarpaceae-*Nothofagus* rainforest.

Compared to other Oligo-Miocene sites on granite in northeast Tasmania, e.g. Pioneer (Hill & Macphail 1983), subcanopy angiosperms with thermophilous NLRs are very rare, such as *Sapotaceoidaepollenites rotundus* (Sapotaceae), or else completely absent as in the case of *Bluffopollis scabratus* (Strasburgeriaceae), *Cupanieidites orthoteichus* (Cupanieae), and *Quintiniapollis psilatispora* (*Quintinia*). One exception is *Myrtaceidites verrucosus* (*Rhodamnia*-type), but the overall impression is of a temperate rainforest community growing under relatively cool (lower mesotherm) conditions.

Paleopalynology —

Standard laboratory treatments were used for the recovery of palynomorphs for palynological dating from the dated samples. This process involves removal of inorganic mineral material by the initial dissolution of the rock in hydrochloric and hydrofluoric acids, followed by heavy-liquid (density) separation of the particulate organic matter from any remaining undissolved mineral matter using zinc bromide solution. From the organic-residue recovered in the float, separate unfiltered and >10µm filtered kerogen slides were prepared for each productive sample. The remaining residues were then oxidised using *Schultz* solution followed by an equivalent short treatment in hot ammonia solution and the final oxidised residues additional slides were prepared filtered at >10µm.

For all samples 250 identifiable pollen and spores (or more) were counted as the pollen sum, and then miospores of individual taxa calculated as a percentage of the total pollen and spore count excluding fungal spores. Values of less than 1% of the pollen sum were counted as a '+' in the pollen count (Table 2) while any remaining rare taxa are recorded outside the pollen count, and denoted in the table with an 'x'.

Macrofossil preparation and identification —

Fossil fruits were mounted on aluminium stubs for scanning electron microscopy and coated in carbon. In total there are 11 fossil fruits, given the specimen codes GF001 through to GF011. These fossils are stored in the David T. Blackburn Palaeobotany collection, at the University of Adelaide.

Extant *Metrosideros* fruits were collected and observed for comparison, from vouchers in the National Herbarium of New South Wales, and the Australian National Herbarium in Canberra (Accession numbers in appendix 1).

Fossil fruits were first observed under a Philips XL30 FEG field emission scanning electron microscope (FEI, Eindhoven, Netherlands), and then fossil and extant fruits were photographed under an Auto-montage Visionary Digital BK+ imaging system with a Canon EOS 7D 18 megapixel camera. Images were produced using PMax image stacking in Zerene Stacker, PMax software (Zerene Systems LLC, Richland, Washington, USA) and cropped and resized in Adobe Photoshop CS6 21 (Adobe Systems Inc., San Jose, CA, USA).

The fossil taxon is identified using a Nearest Living Relative (NLR) approach. General taxonomy of the Myrtaceae follows Wilson (2011). Specific *Metrosideros* taxonomy follows Dawson (1970a, 1976, 1984).

Table 2: Stratigraphic distribution and relative abundance data. Values for samples yielding over 250 identifiable pollen and spores are calculated as a percentage of the total pollen and spore count excluding fungal spores. '+' indicates values less than 1%. Raw counts are given in parentheses for samples yielding <250 pollen and spores. 'x' indicates rare species recorded outside the pollen count.

Fossil Equivalent	Nearest Living Equivalent	Golden Fleece Rivulet (m AHD)			
		+1.55	-0.25	-0.35	-0.75
Exotic taxa					
Pinus	*Pinus*	+	+	+	x
Asteraceae (Liguliflorae)	Cichorieae	+			
Polygonum aviculare-type	Polygonum aviculare	x			
Algae					
Circulisporis parvus	Zygnemataceae	+			x
Amorphous &unassigned types	unknown		(abund)		
Fungi					
Pesavis	-			x	x
Spores and hyphae	-	34%	(12)	165%	310%
Mosses and liverworts					
Baculatisporites disconformis	Hymenophyllaceae			x	+
Baculatisporites cf *scabridus*	Hepaticae?				x
Baculatisporites sp.	Hepaticae	x	(3)	2%	4%
Cingulatisporites bifurcatus	*Phaeoceros* (Anthocerotae)	x			
Cingutriletes/Stereisporites australis	Sphagnaceae			x	x
Densoisporites implexus	*Selaginella uliginosa*	x			
Herkosporites elliottii	*Lycopodium deuterodensum*			x	
Latrobosporites marginis	*Lycopodiella lateralis*	x			
Pilularia-type	Marsileaceae	x			
Rudolphisporis rudolphi	*Anthoceros* (Anthocerotae)	x			x
Ferns & fern allies					
Baculatisporites disconformis	Hymenophyllaceae			+	+
Cyatheacidites annulatus	*Lophosoria*			+	x
Cyathidites australis/paleospora	*Cyathea*	1%	(4)	+	+
Cyathidites cf. *splendens*	Cyatheaceae?			x	x
Cyathidites cf. *subtilis*	*Cyathea*		x		
Gleicheniidites spp.	Gleicheniaceae	x			
Hypolepis australis	*Hypolepis*	1%			
Ischyosporites cf. *lachlanensis*	unknown			x	+
Laevigatosporites ovatus/major	includes Blechnaceae	3%		1%	x
Matonisporites ornamentalis	*Dicksonia antarctica*	56%	(5)	2%	2%
cf. *Matonisporites ornamentalis*	immature *Dicksonia* spores?	15%	x	x	x
Peromonolites baculatus ms	Blechnaceae?			1%	x
Peromonolites densus	Blechnaceae?			x	x
Peromonolites vellosus	Blechnaceae?			x	x
Polypodiisporites histiopteroides	*Histiopteris*	3%			
Polypodiisporites spp.	includes *Microsorium*	4%			
Retitriletes austroclavatidites	*Lycopodium*			x	x
Rugulatisporites mallatus	*Calochlaena*	x			x
Rugulatisporites trophus	*Calochlaena*	x			
Trilites tuberculiformis	Dicksoniaceae			x	+
Verrucosisporites cristatus	unknown			x	x
Verrucosisporites kopukuensis	unknown			x	
unassigned spores	(numerous families)	3%		2%	+
Gymnosperms					
Araucariacites australis	*Araucaria*		(1)	+	+
Cupressacites	Cupressaceae-Taxodiaceae				
Dacrycarpites australiensis	*Dacrycarpus*			x	x
Dacrydiumites florinii	*Dacrydium*			+	+
Dilwynites granulatus	*Agathis/Wollemia*			+	
Microcachryidites antarcticus	*Microcachrys*				x
Microalatidites palaeogenicus	*Phyllocladus*	x		+	1%
Phyllocladidites mawsonii	*Lagarostrobos franklinii*		(1)	1%	2%
Podocarpidites spp.	*Podocarpus*	x	(3)	14%	9%
Podosporites erugatus	*Pherosphaera*				x
Podosporites parvus/microsaccatus	extinct Podocarpaceae			+	+

Table2 (cont):

Fossil Equivalent	Nearest Living Equivalent	Golden Fleece Rivulet (m AHD)			
		+1.55	-0.25	-0.35	-0.75
Angiosperms					
Acaciapollenites myriosporites	*Acacia*	x	(1)		
Banksieaeidites cf. *elongatus*	*Banksia*	x			cf.
Chenopodipollis chenopodiaceoides	Chenopodiaceae	+			
Cunoniaceae	Cunoniaceae				x
Cyperaceaepollis spp/	Cyperaceae	x			+
Dodonaea viscosa-type	*Dodonaea viscosa*-type			cf.	
Dryadopollis retequetrus	extinct clade?			x	
Ericipites spp.	Epacridaceae	9%		+	x
Graminidites	Poaceae	x	(1)		
Gyropollis psilatus	Gyrostemonaceae	x			
Haloragacidites haloragoides	*Haloragis/Gonocarpus*	+			
Haloragacidites harrisii	Casuarinaceae	8%	(45)	+	+
Leucopogon-type	*Leucopogon*	x			
Liliacidites bainii	Arecaceae/Liliaceae			x	
Liliacidites spp.	Arecaceae/Liliaceae			x	+
# *Malvacipollis subtilis*	*Austrobuxus*			x	+
Milfordia hypolaenoides	Restionaceae	+			
Monotocidites galeatus	*Monotoca*	x			
Mutisiapollis cf. *patersonii*	*Mutisia*				x
Myrtaceidites eucalyptoides	*Eucalyptus* sensu lato			x	
Myrtaceidites parvus-mesonesus	Myrtaceae			+	x
Myrtaceidites aff. *leptospermoides*	*Melaleuca*-type		(1)		
cf. *Myrtaceidites lipsis*	*Eucalyptus spathulata*?	x			
Myrtaceidites verrucosus	*Rhodamnia*-type				x
Nothofagidites asperus	*Nothofagus* (*Lophozonia*)			2%	2%
Nothofagidites brachyspinulosus	*N.* (*Fuscospora*) spp.		(4)	6%	6%
Nothofagidites falcatus	*N.* (*Brassospora*) sp.			+	+
Nothofagidites emarcidus-heterus	*N.* (*Brassospora*) spp.	+	(19)	59%	65%
Nothofagidites flemingii	*N.* (*Nothofagus*) spp.			x	
Periporopollenites demarcatus	Trimeniaceae			+	
Poluspissusites ramus	Goodeniaceae				cf.
Polyporina granulata	*Stellaria*	x			
Proteacidites obscurus	cf. *Agastachys*			x	x
Proteacidites pseudomoides	extinct? clade Proteaceae			x	x
Proteacidites scaboratus	extinct? clade Proteaceae			x	x
Proteacidites rectomarginis	extinct clade Proteaceae				x
Proteacidites spp.	Proteaceae	x		+	+
Rhoipites ampereaformis	*Amperea*	4%			
Rhoipites sp.	numerous taxa	x			x
Sapotaceoidaepollenites rotundus	Sapotaceae				x
Tetracolporites cf. *palynius*	extinct? clade				x
Thymelaepollis sp.	*Pimelea*	x		x	x
Tricolpites reticulatus	Gunneraceae			x	x
Tricolpites/Tricolporites	numerous taxa	x		+	1%
Tricolporopollenites chnosus	extinct clade Proteaceae?			x	x
Tubulifloridites antipoda/simplis	Asteraceae	x			
POLLEN SUM		**295**	**(85)**	**388**	**382**
REWORKED TAXA					
Jurassic-Cretaceous (*Annulispora folliculosa*)					x
Jurassic (*Nevesisporites redunctus*)					x
Permian *(Plicatipollenites sp)*				x	
Devonian? spore		x			

DESCRIPTION

There is a great deal of morphological variation among the fossil fruits presented. All of the fossil fruits are between 2- 3mm in length, and between 1.5-2.5mm in width (Fig. 3). The fruits have all been significantly flattened during fossilization, and so these measurements may be a slight over-estimate of their true size. All of the fossil fruits appear to be three-locular capsules, with at least some free part of the capsule exserted from the hypanthium. However, we conclude that there are two different taxa represented by these fruits.

Metrosideros fruits described by Pole et al. (2008) (Fig. 4C,D), although these veins are more strongly developed, and the valves less strongly defined as the fruit does not appear to have reached maturity and dehiscence. In Fig. 4B the external side of the middle valve (valve 2) can be clearly seen. While there is some cracking and breakage of the lower half of specimen E, the valve is intact, and there is a clear groove running up the middle of the valve, which terminates in a shallow groove in the top of the valve. This indicates the point of style insertion, in a shallow pit on the summit of the ovary.

Taxon 1 —

Specimen E possesses the most obvious characters. The capsule of the fruit is exserted beyond the hypanthial rim, making up nearly a third of the length of the fruit. The fruit is pentamerous, with the sepals inserted on a prominent hypanthial rim which appears as a swollen 'lip' around the capsule. Five persistent veins are visible running up and down the hypanthium, terminating in each of the five sepals (Fig. 4A,B). The presence of only 'five major veins' is a synapomorphy for the tribe *Metrosidereae* (Wilson 1996, 2011), a feature visible in many of the extant fruits used for comparison (Fig. 6). For further comparison, this synapomorphy can also be seen in the mummified, Miocene aged

Taxon 2 —

The second taxon (Fig. 3 A,B,C,D & F), possesses sepals that are apparent on some specimens, but are highly reduced or residual when compared with the first taxon. The fruits are pentasepalous, and the veins in the hypanthium, terminating in the sepals, are less prominent on these fruits (Fig. 3A,B) than in Taxon 1. The specimens shown in Fig. 3 A & F, with reduced width and size, may represent fruits of this taxon that are less mature.

The specimens shown in Fig. 3B, C, D and to a lesser degree F are 'urn shaped' fruits, with a slight restriction just below the hypanthial rim, with very reduced yet persistent sepals. In some of these fruits (such as Fig. 3 A & F), faint veins can be seen running along the hypanthium and terminating in the sepals, though not as pronounced as in Fig. 3 E. The hypanthial rim is prominent, and appears as a swollen 'lip', particularly in the more mature fruits (Fig. 3B,C,D)

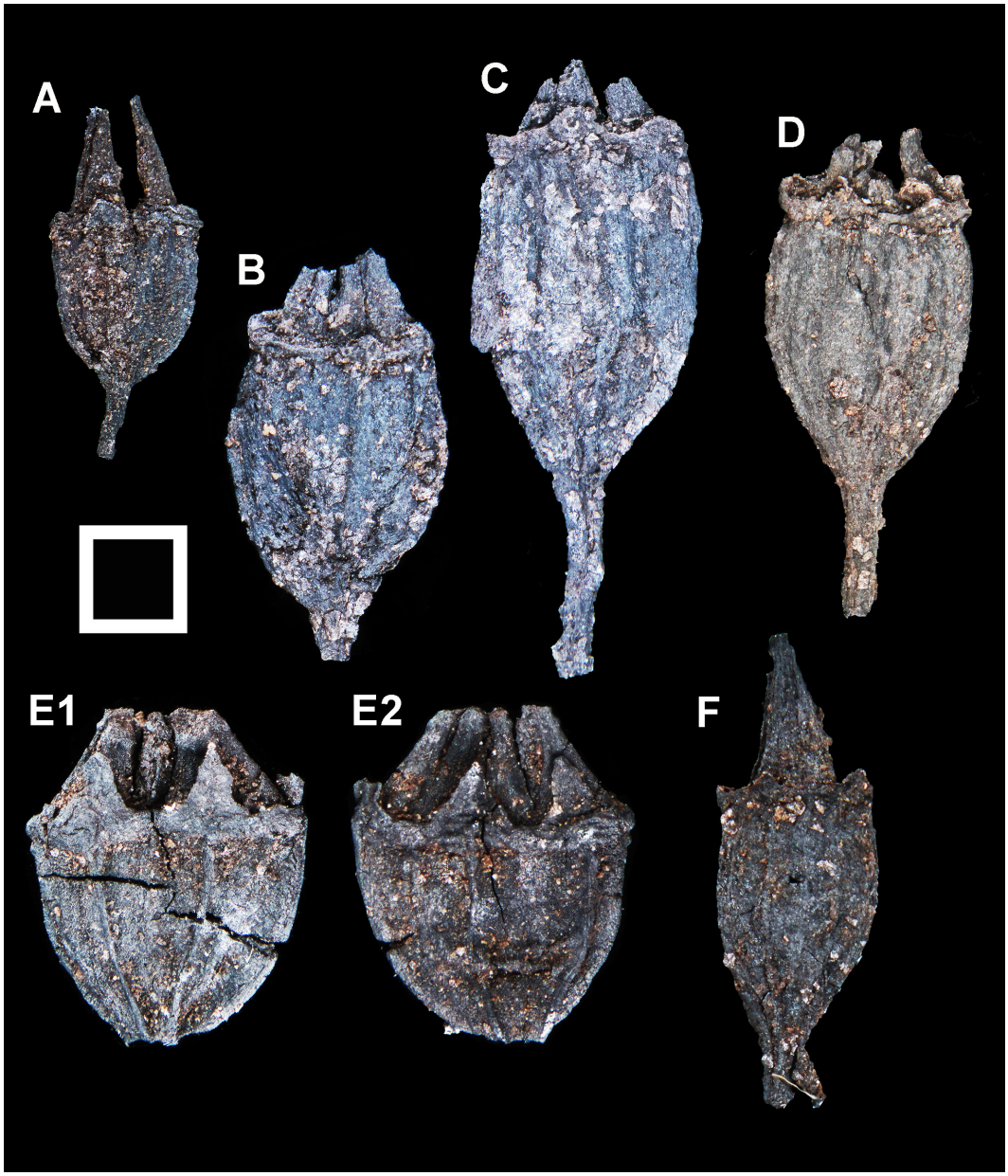

FIGURE 3– Fossils, named by their collection codes, recovered from the Golden Fleece Rivulet **– (A)** GF006 **(B)** GF002 **(C)** GF004 **(D)** GF001 **(E1 & 2)** GF005, (both sides of the fruit), **(F)** GF009. Scale bar = 1mm. x 1mm.

The most unusual character on all of the fruits, and worthy of note, is the thin and attenuated valves of the capsule, which is three parted (Fig. 3A,C&D) ruling out any potential that this structure may represent a persistent style base. In the case of the specimens in Fig. 3 A & F, these valves are very strongly exserted.

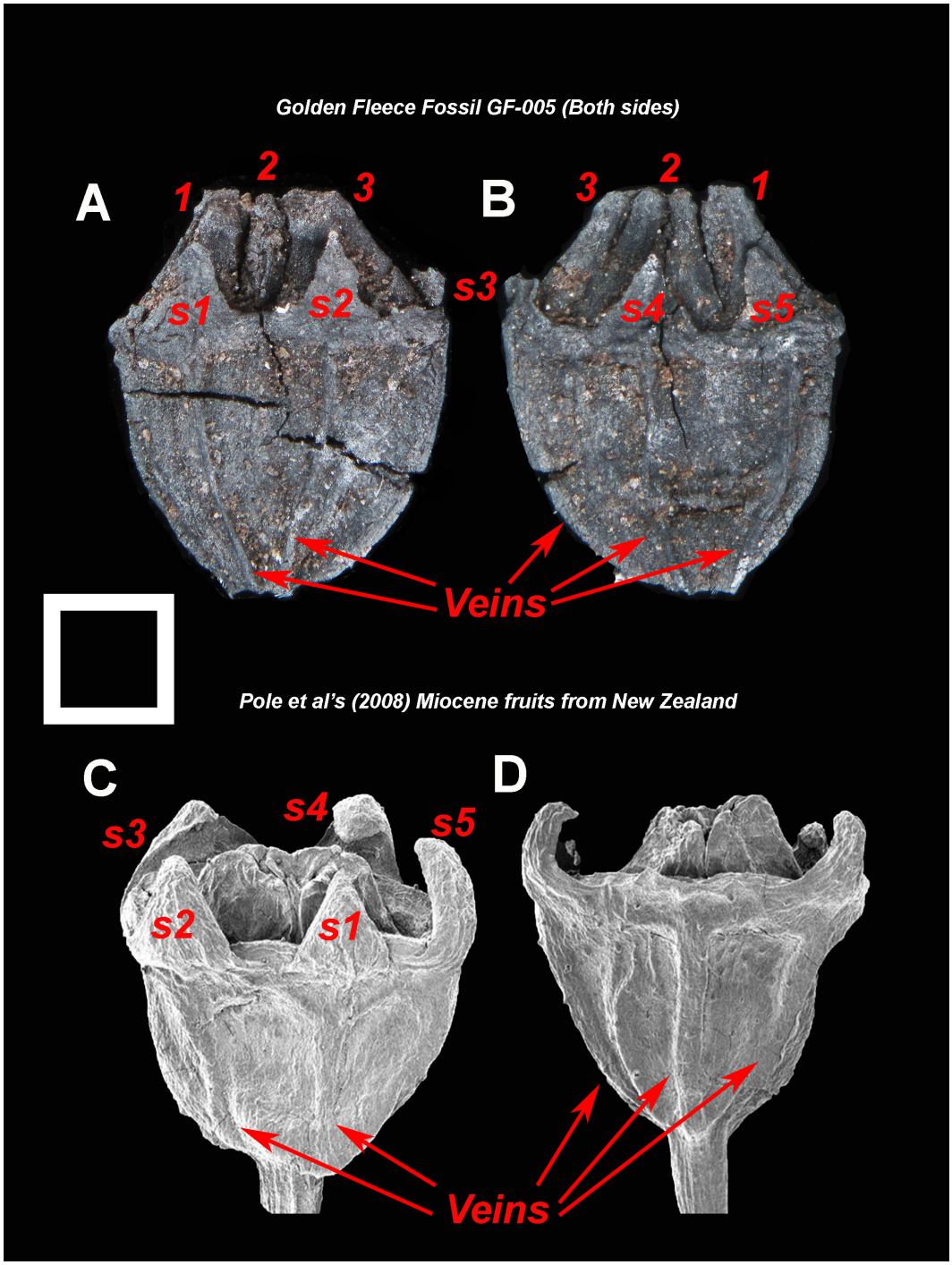

FIGURE 4 – Anatomy of Taxon 1, *Metrosideros dawsonii* sp. nov. – In comparison with fossils found from Miocene of New Zealand by Pole (2008) **– (A & B)** Both sides of fruit GF005 – Valves are denoted 1,2,3 and are shown from both sides of the fruit. Sepals are denoted S1,2,3 etc. Note how the five veins run up the hypanthium and terminate in the sepals. **(C & D)** Fossil *Metrosideros* fruits from the Miocene of New Zealand depicted by Pole (2008) specimens S-1274 & S-1270. Note the same number of sepals and same number of veins. The fruit does not appear to be as mature as GF-005 and valves are not easily distinguishable. Scale bar = 1mm. x 1mm.

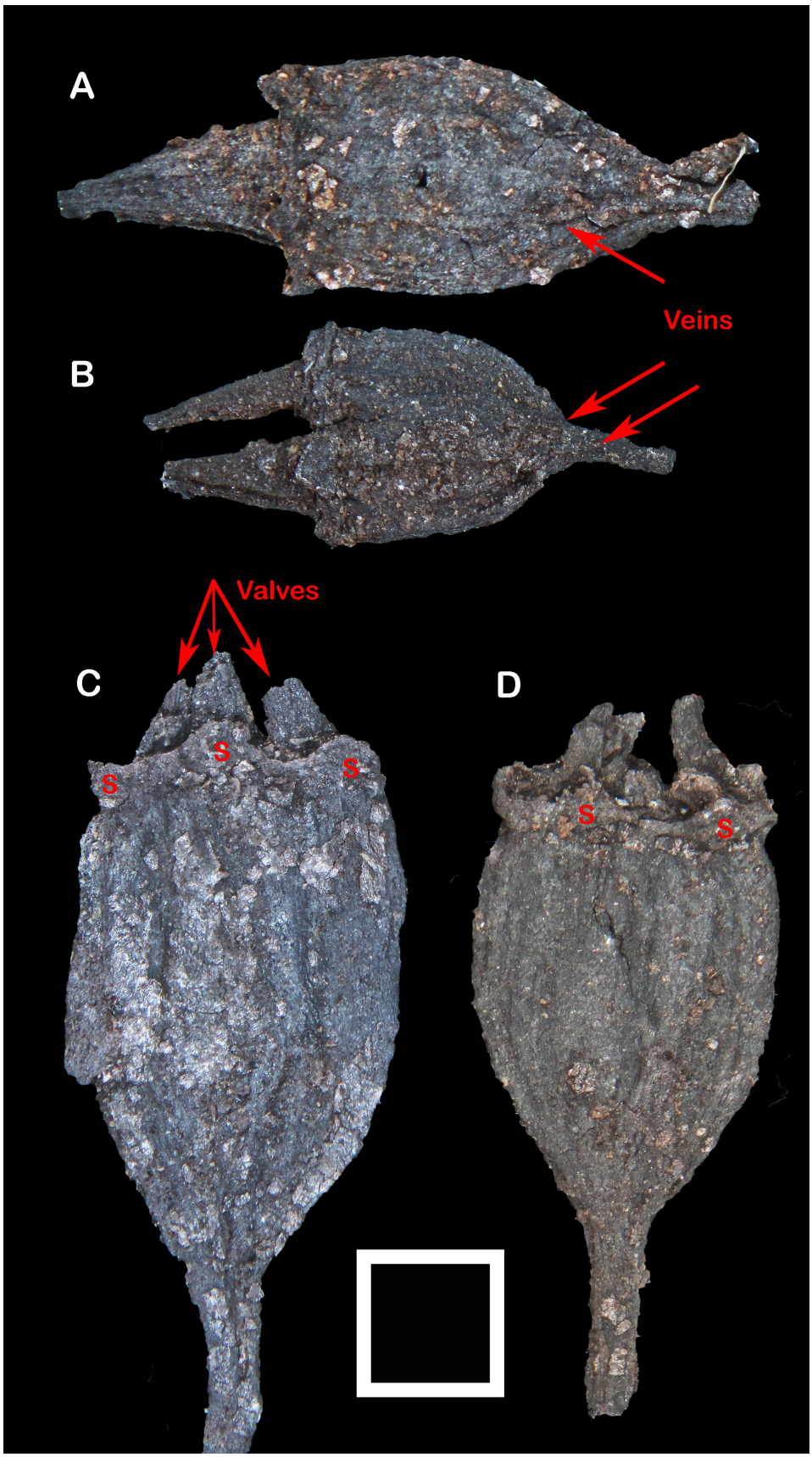

FIGURE 5 – Anatomy of Taxon 2, *Metrosideros wrightii* sp. nov. – **(A)** GF006 **(B)** GF009 **(C)** GF004 **(D)** GF001. Note the veins denoted by arrows in specimens **A & B** are feint, but recognisable. Valves are demonstrated on specimen **C**, and the reduced sepals (S) are denoted on specimens **C & D.** Scale bar = 1mm. x 1mm.

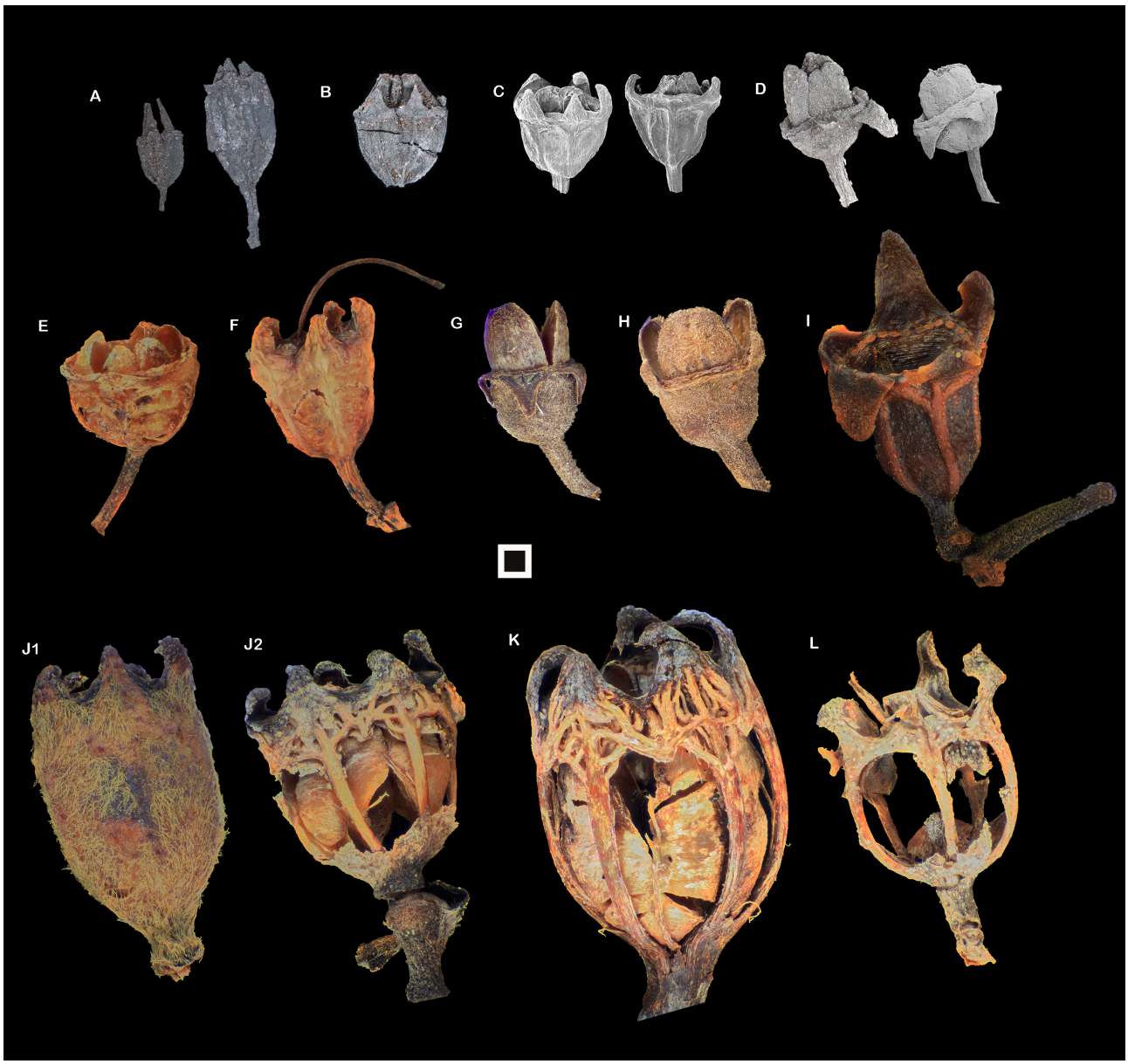

FIGURE 6 – A collection of *Metrosideros* fossils in comparison with extant taxa**; (A)** *M. wrightii* sp. nov. **(B)** *M. dawsonii* sp. nov. **(C)** Pole et al's (2008) *Metrosideros* fossils from the Miocene of New Zealand, **(D)** *M. leunigii,* the Little Rapid River fossils described in Tarran et. al. (2016) **(E)** *Metrosideros angustifolia* **(F)** *Tepualia stipularis* **(G)** *Metrosideros bartlettii* **(H)** *Metrosideros robusta* **(I)** *Metrosideros cherrieri* **(J1 & 2)** *Metrosideros punctata*, two fruits at different stages of decomposition, showing highlighting the prominent five major veins **(K)** *Metrosideros sclerocarpa* **(L)** *Metrosideros operculata*. Scale bar = 1mm. x 1mm.

SYSTEMATICS

TAXON 1 —

Order: Myrtales
Family: Myrtaceae
Tribe: Metrosidereae
Genus: *Metrosideros*
Species: *Metrosideros dawsonii* sp. nov.
Etymology: Named for John W. Dawson, in recognition of his work illustrating and classifying the extant Pacific capsular-fruited Myrtaceae.

Diagnosis: Fruit a small, loculicidal capsule, strongly exserted from the fruiting hypanthium when mature. Ovary 3-locular, loculicidally dehiscent capsule with style inserted in a shallow pit on the summit. Flower 5-merous. Sepals deltoid, inserted on the prominent hypanthial rim, which appears as a swollen 'lip' around the capsule. Five main, persistent hypanthial veins, terminating in the sepals.

Holotype: GF-005

TAXON 2 —

Order: Myrtales
Family: Myrtaceae
Tribe: Metrosidereae
Genus: *Metrosideros*
Species: *Metrosideros wrightii* sp. nov.

Etymology: Specific epithet for Shane Wright, in recognition of all of the work he has done contributing to understanding the biogeography and evolution of *Metrosideros.*

Diagnosis: Fruit a small, loculicidally dehiscent capsule, slightly exserted from the fruiting hypanthium when mature. Ovary 3-locular. Flower 5-merous. Locules of the capsule attenuated. Sepals persistent, highly reduced, inserted on the prominent hypanthial rim, which appears as a swollen 'lip' around the capsule. Five main, persistent hypanthial veins, terminating in the sepals.

Holotype: GF-004
Paratype: GF-001**.**

DISCUSSION

Justification for assignment to genus —

Several synapomorphies on the fossil fruits, particularly in combination, can be used to confidently diagnose these fossils as belonging to the Myrtaceae, and then to the genus *Metrosideros*:

1) *Loculicidally-dehiscent, tricarpellate ovary* - Both taxa, *Metrosideros dawsonii* and *Metrosideros wrightii* can be confidently assigned to the Myrtaceae due to the presence of a diagnostic set of characters. The ovary is tricarpellate, and partially exserted beyond the hypanthial rim upon maturity of the fruit, which is a dry, loculicidally-dehiscent capsule. The fruit in all cases is pentasepalous, which indicates pentamery. These characters are highly consistent with assignment to the Myrtaceae, and are particularly suggestive of the tribes Kanieae and Metrosidereae (Basinger et al., 2007; Tarran et al., 2016).

2) *Five main veins in the hypanthium* - The most important character for identification for both fossil taxa is the presence of five main veins in the hypanthium, terminating in the sepals. This is a synapomorphy for the tribe Metrosidereae as defined by Wilson (2011). It is not the case that the fruits of all Metrosidereae ONLY have five veins, but that there are five major vascular traces. Remnants of the tops and bottoms of intermediate, non-major veins can be seen between the main veins in some extant *Metrosideros* post-dehiscence (Fig. 6 J2,K). The character of five, persistent and highly conspicuous externally visible veins running along the hypanthium is a feature commonly seen in the genus *Tepualia* (Dawson, 1972b), and the (formerly) broadly defined *Metrosideros* subgenus *Mearnsia* (Dawson, 1970b, 1972a) (Fig. 6). It is now unlikely that what has been called subgenus *Mearnsia* is a monophyletic group (Pillon et al., 2015), so we cannot suggest subgeneric affinities other than to comment that they do not have any characters which suggest placement in subgenus *Metrosideros,* as we could with *M. leunigii* (Tarran et al., 2016).

The character of five main veins occurs in all *Metrosidereae* (Wilson, 2011), though they are not always 'strongly developed' and hence visible on the fruit externally, such as in many of the extant taxa within the broadly defined subgenus *Metrosideros* (See Fig. 6) and as such this was not a character used for identifying *M. leunigii* from Oligocene sediments at Little Rapid River in Tasmania (Tarran et al., 2016). The character of five prominent veins visible in the hypanthium is largely consistent with the formerly recognised subgenus *Mearnsia*, or at least it is inconsistent with most of the species in the subgenus *Metrosideros,* which often have more weakly developed veins (See Fig. 4D, F &G), that are not always visible without skeletonising or sectioning the fruit. The character was a critical one for Wilson (1993) in demonstrating that the phylogenetic placement of *Metrosideros queenslandica* (the only species on the Australian mainland referred to *Metrosideros* at the time) was incorrect. From this reassessment,

the species was referred to the tribe *Tristanieae,* and renamed *Thaleropia queenslandica.*

Even in the species with more strongly developed veins, largely in the formerly recognised subgenus *Mearnsia,* the veins are not always highly visible on the surface of the hypanthium. For example, in *Metrosideros punctata* J.W. Dawson (Fig. 6 J1,2) this character is only clearly visible in the later stages of fruit maturity, where the thinner parts of the hypanthium break down between the five thickened major veins.

3) *Hypanthial rim* – A further character which was used by Tarran et al. (2016) to identify *M. leunigii* from other closely related capsular fruited Myrtaceae in the tribe Kanieae, was the prominent hypanthial rim, which appears as a swollen lip. This character was observed in many *Metrosideros* species, and found lacking in many species from the tribe Kanieae. It was observed that in the treatment of the groups that would later become the two subgenera of *Metrosideros*, Dawson (1970a, b, 1976) notes that the stamens are "*in a single whorl, set behind the rim formed distally from the hypanthial lining*," and in some cases, in the *Mearnsia* group, "*arising directly from it".* He considered this to be an important character. While stamen scars are not visible on any of the Golden Fleece *Metrosideros* fossils, unlike *M. leunigii,* the swollen hypanthial rim is a strong indicator of *Metrosideroid* affinity.

4) *Insertion of style base in the ovary* - Additionally, *Metrosideros dawsonii* has a shallow groove running down the middle of the valve, denoting the boundary of the carpel, which terminates in a 'v' shaped groove at the top of the valve. This is seen in many modern representatives of *Metrosideros,* and evidences the point of style insertion in a shallow pit in the summit of the ovary where the 'v' shaped grooves at the top of each valve meet. This is particularly visible on the valves of *M. angustifolia* (L.) Sm. pictured in Fig. 5D. This character was one of the final characters used by Tarran et al. (2016) to describe *M. leunigii,* as it can help distinguish Metrosidereae fruits from those of the Kanieae, because the latter often have the style terminal on the ovary summit, rather than being inserted in a shallow pit.

Worthy of note is the large degree of superficial resemblance between *M. dawsonii* and the oldest (Miocene) fossil *Metrosideros* fruits from New Zealand illustrated by Pole et al. (2008) which were never formally described. The similarity between these fossils is greater than between either of the described fossils and any extant taxon. Pole et al. (2008) makes a comparison of their Miocene fossils with the New Caledonian species *M. operculata* and *M. patens,* both belonging to the formerly recognised subgenus *Mearnsia.* Interestingly, the two characters of: **1)** the five persistent, visible, hypanthial veins terminating in the sepals, and **2)** the locules of the ovary being exserted well beyond the hypanthial rim; do not occur in combination in either of the extant species that Pole et al. (2008) illustrates and compares with those fossil fruits. We observe here that these two characters are not

found in combination in any modern representatives of *Metrosideros* in New Zealand, and are not observed in any extant species of the formerly recognized subgenus *Mearnsia.*

Subtle character differences, such as the difference in thickness of the five hypanthial veins, and the difference in size of sepals, between *M. dawsonii* and the undescribed fruits illustrated by Pole et al. (2008) make us reluctant to formally assign those specimens to the same fossil species, especially without personally examining the Pole et al. (2008) fruits. Nevertheless, the similarities are striking and we suggest that the Pole et al. (2008) undescribed *Metrosideros* fruits and *M. dawsonii* potentially represent a closely related lineage that is now extinct from both Australia and New Zealand

Metrosideros wrightii is even more unusual, with its long acuminate valves. This character has not been observed in any modern *Metrosidereae.* The closest example of such acuminate valves is in some species of *Eucalyptus,* such as *E. socialis* F.Muell. ex Miq. However, in the case of *E. socialis* the acuminate valves are derived from a persistent style base, rather than a conical capsule summit.

Paleobiogeography —

This is the second record of fossil *Metrosideros* species from the Cenozoic of southeastern Australia, and both taxa described here represent different species to those described from the Early Oligocene sediments at Little Rapid River (Tarran et al., 2016). The fossil record of the capsular fruited Myrtaceae has been called 'largely equivocal' (Basinger et al., 2007), but the fossil record of *Metrosideros* in southeastern Australia, along with Basinger's record of Kanieae in South Australia is beginning to highlight that the Myrtaceous component of the Cenozoic Southeastern Australian vegetation differed markedly from the present day flora. Clearly these closely related capsular-fruited groups, the Kanieae and Metrosidereae, were once much more widely spread in Australia than they are today, with the Metrosidereae now entirely extinct in Australia, and the Australian distribution of Kanieae now mostly restricted to the Eastern margins of Australia (particularly the genera *Baronigia, Sphaerantia, Ristantia, Mitrantia* and *Tristaniopsis*) or else to the tropics of Papua New Guinea and surrounding landmasses in the Indonesian archipelago (*Kania, Basisperma, Tristaniopsis*) or New Caledonia (*Tristaniopsis, Cloezia*) (Basinger et al., 2007; Wilson, 2011)

Wilson (1996) proposed that New Zealand was the landmass where the two subgenera of *Metrosideros* first diverged and Wright et al. (2000) hypothesized that a lack of a fossil record on other Gondwanic landmasses, plus a 'long fossil record' in New Zealand, pointed towards a New Zealand origin for the genus. Contrary to this, Tarran et al. (2016) proposed an Australian origin for the genus. The fossils reported here, in conjunction with those described previously, establish that *Metrosideros* was not only present in Australia, but there was some diversity of species, and these may have persisted in the vegetation from the Eocene-Oligocene, to at least the Oligo-Miocene.

Making any inferences of infra-generic paleobiogeography is difficult since the relationships within *Metrosideros* at this taxonomic level are poorly resolved (Pillion et al. 2015). It now seems that while the subgeneric classification of subgenus *Metrosideros* represents a monophyletic lineage, subgenus *Mearnsia* is not a monophyletic group, and there could not have been a single divergence event between the subgenera *Metrosideros* and *Mearnsia.*

The fossils described in this study are of a similar age to those described by Pole et al. (2008) and are strikingly similar in superficial appearance. While subgenus *Mearnsia* species do occur in New Zealand, none exist with such strongly defined persistent hypanthial veins. Pole (2008) notes that these fruits do not bear close resemblance to any of the extant New Zealand genera of either subgenus *Metrosideros* or subgenus *Mearnsia,* and suggested the fossils most closely resembled species of subgenus *Mearnsia* from New Caledonia and Papua New Guinea.

While it is apparent that the traditional subgeneric groupings may not hold up to phylogenetic scrutiny, they may still hold some value for paleobiogeographic interpretation, since it is only the subgenus *Metrosideros* that is widely distributed around the Pacific, probably due to their lightweight and highly vagile seeds (Corn, 1972; Drake, 1992; Wilson, 1996). Therefore it is feasible that any given fossils of subgenus *Metrosideros* in Australia might represent taxa that arrived via long distance dispersal, rather than vicariance and, as such, it is not possible to say with certainty that the fossils of *M. leunigii* described by Tarran et. al. (2016) support an Australian origin of the genus. On the other hand, what was called subgenus *Mearnsia* (now just the remaining species in the genus) is more restricted in its distribution than subgenus *Metrosideros*, occurring only on the Gondwanic landmasses of New Zealand, New Caledonia, New Guinea, as well as the Solomon Islands and the Philippines. As such, the fossil species *M. dawsonii* and *M. wrightii,* which do not recognizably belong to the subgenus *Metrosideros,* and may share affinities with members of the formerly recognized *Mearnisa* group, are more likely to represent long-standing vicariant populations.

The superficial resemblance of both *M. dawsonii,* and even more of Pole et al's (2008) undescribed fruits, to *Tepualia stipularis* (or *Metrosideros stipularis* if the most recent circumscription by Pillon et al. (2015) is accepted), is also worthy of comment (See Fig. 6F). Analyses by Wilson (1996) and Thornhill et al. (2015) show that *Tepualia* is sister to much of the Metrosideroid diversity. Prior to this most recent circumscription of the genus, Thornhill et al. (2015) speculated that the disjunction between the occurrence of *Tepualia* in South America and *Metrosideros* in the rest of the Pacific, from New Zealand to New Caledonia, Hawaii and South Africa, might have arisen in a number of ways: (1) through extinction of *Metrosideros* in South America, (2) extinction of *Tepualia* in New Zealand, (3) a long distance dispersal event of *Metrosideros* from New Zealand to Africa, or (4) the extinction of a more widespread ancestor leaving its relicts in South America and Africa. The long fossil record of *Metrosideros* now found in Australia may be considered evidence for this final option.

Finally, it is interesting to consider why *Metrosideros* became extinct in Australia. It is likely that this extinction occurred during the time of extreme rainforest contraction in the Neogene and early Quaternary, as Australian climates became drier and fires became more widespread and frequent (Byrne et al. 2011; Hill, 2004). Extant *Metrosideros* species now largely occur on islands that, prior to human arrival had relatively few fires, but also often no mammalian browsers. The hypothesis that aridification was a direct driver of the extinction of *Metrosideros* from Australia is relatively weak, because the species extend to relatively dry climates today. More likely is that fire was important, and it is also possible that evolution of large mammalian browsers may have contributed to the loss of *Metrosideros* from Australia. In New Zealand, the preferential browsing of *Metrosideros* spp. by invasive possums is a significant conservation concern, and in some cases has lead to significant dieback of forests (Batcheler, 1983). These hypotheses for extinction in Australia may be tested with more detailed analysis of the improving fossil record of the tribe, especially taking phylogeny and functional traits into account.

CONCLUSIONS

The discovery of *M. dawsonii* sp. nov. and *M. wrightii* sp. nov. establishes the presence of two species of *Metrosideros* in the Oligo-Miocene of Tasmania, without clear affinities to the more widely spread subgenus *Metrosideros*. Although *Metrosideros* is no longer present in Australia today, this new fossil evidence, combined with the fossils described in Tarran et al. (2016), demonstrate that not only was *Metrosideros* once present in Australia during the Cenozoic, but that a diversity of *Metrosideros* species persisted at least from the Eocene-Oligocene of southeastern Australia into the Oligo-Miocene. This further strengthens the hypothesis previously put forward by Tarran et al (2016), of an Australian origin of the genus, and further adds to the mystery of its extinction on the continent.

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